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Fossil Curtonotidae (Diptera: Schizophora: Ephydrioidea)

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ABSTRACT

Curtonotidae are a small, mostly tropical family of acalyprate flies in the Ephydrioidea, a superfamily that also includes the Drosophilidae. Two species of Curtonotidae are described from Miocene amber of the Dominican Republic, 17–20 Ma: *Curtonotum †electrodominicum* Grimaldi and Kirk-Spriggs, sp. n., and *Depressonotum †priscum* Grimaldi and Kirk-Spriggs, gen. et sp. n. The fossil *Curtonotum* is based on a female specimen and has some features of Neotropical species and a small clade of African species. *Depressonotum †priscum*, gen. et sp. n., is based on a male and female and has a unique combination of features that are plesiomorphic and derived for the Curtonotidae. These are the only definitive fossils of the family and the only Curtonotidae known from the Caribbean. The fossil Curtonotidae provide rare data on the geological occurrence of ephydroid flies, essential for estimates of divergence times.

INTRODUCTION

The superfamily Ephydrioidea is generally considered to comprise five families, each of which is cosmopolitan or virtually so: the well-known Drosophilidae (vinegar flies), the ubiquitous Ephydriidae (shore flies), and the smaller, lesser known families Diastatidae (including Campichoetinae), Camillidae, and Curtonotidae (Hennig, 1958; McAlpine, 1989; Chandler, 1987; Grimaldi, 1990). Wiegmann et al. (2011) provided a phylogenetic estimate of fly relationships based on combined molecular and morphological data from 149 of the 157 families worldwide. In a result that differs

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from previous interpretations based on morphology alone, this study indicated that (Drosophilidae + Braulidae + Cryptochetidae) are sister to the remainder of the Ephydrioidea (Camillidae + (Curtonotidae + Diastatidae)), except for the Ephydriidae. Kirk-Spriggs et al. (2011) concluded that the structure of the reproductive tract of Mormotomyiidae lends support to the inclusion of that family in the Ephydrioidea and McAlpine (2011) further noted that the general structure of the antenna supports this hypothesis. These recent hypotheses are very interesting since Braulidae are wingless, eyeless, highly specialized inquilines in the nests of *Apis* honeybees (Grimaldi and Underwood, 1986), and Mormotomyiidae are likewise highly specialized, wingless symbionts, but on bats.

The vernacular “Quasimodo flies” has been applied to Curtonotidae (Kirk-Spriggs, 2010a, 2010b; Kirk-Spriggs and Wiegmann, in prep.) in reference to the hunchbacked thorax of extant species. Compared to Drosophilidae (ca. 3400 described species) and Ephydriidae (ca. 1800 species), Curtonotidae are a small family, currently comprising 93 species in four genera. The genera are *Axinota* van der Wulp (12 species in Asia, the Middle East, and Afrotropical region), *Tigrisomyia* Kirk-Spriggs (4 species from Afromontane forests of East Africa), *Curtonotum* Macquart (73 species, from all regions, except Australasia and Pacific Oceania, and including species soon to be described by Kirk-Spriggs and Wiegmann, in prep.), and *Cyrtona* Séguy sensu lato (5 species, from the Afrotropical region). Systematics of the family has recently attracted intensive study (Kirk-Spriggs, 2008a, 2008b; 2010a, 2010b; 2011; Kirk-Spriggs and Freidberg, 2007; Kirk-Spriggs and Wiegmann, in prep.; Klymko and Marshall, 2011); prior major studies include Delfinado (1969) for the Oriental region and Tsacas (1974, 1977) for the Afrotropical.

The little that is known regarding the life histories of these flies is based largely on some species of *Curtonotum*. Several Afrotropical species have been bred as scavengers from the damaged egg masses of Acrididae (Orthoptera) (Greathead, 1958; Kirk-Spriggs, 2008b) and a Nearctic species has been reared under laboratory conditions on the same substrate (Meier et al., 1997). Adults of many species in arid regions of Africa inhabit small mammal burrows. The adults of some Neotropical species are attracted to dung and a species from Peru was bred from a nest of the sphecid wasp *Philanthus* (Hymenoptera: Crabronidae) that was stocked with bee prey (Klymko and Marshall, 2011).

The only fossil attributed to Curtonotidae, until now, is *Curtonotum †gigas* Théobald, a compression in Early Oligocene shale from Les Camoins, Provence, France (Théobald, 1937). Kirk-Spriggs (2007) reexamined this specimen and concluded it was not Curtonotidae. Thus, the two species described here are the only definitive fossils of the family and, interestingly, the only Curtonotidae (living or fossil) known from the Caribbean. Fossil Ephydrioidea occur in fossilized resins from the Eocene to the Holocene, many of which are in mid-Eocene (Ypresian) Baltic amber. These are as follows: three described stem-group species of Diastatidae (*Pareuthychaeta* Hennig) in Baltic amber and in earliest Eocene Cambay amber from western India (Hennig, 1965; Grimaldi and Singh, 2012); two described stem-group species of Camillidae (*Protocamilla* Hennig) in Baltic amber (Hennig, 1965; Grimaldi, 2005); several undescribed species in two modern genera of Ephydriidae in Dominican amber (Grimaldi, unpubl.); and one stem-group species of Drosophilidae described from Baltic amber (Hennig, 1965). Diverse Drosophilidae (described and undescribed) exist in Miocene amber from Chiapas, Mexico, and the Dominican

Republic, and several species in Holocene copal from Tanzania and Kenya (Grimaldi, 1987; 1989; unpubl.). Only basal, non-Schizophora Cyclorrhapha are known from the Cretaceous (Grimaldi and Cumming, 1999; Grimaldi and Engel, 2005; Grimaldi, unpubl.). Thus, it is highly unlikely that Ephydriodea, and particularly Curtonotidae, are any older than Paleocene.

MATERIALS AND METHODS

The amber specimens used for this study were purchased from Susan Hendrickson and Manuel Perez in the 1990s, and originally derived from amber mines in the north-central range of mountains (Cordillera Septentrional) of the Dominican Republic, 20–30 km northeast of Santiago (Grimaldi, 1995). Age of the amber has been estimated on the basis of stratigraphy to be mid-Miocene in age, 15–20 Ma (Iturralde-Vinent and MacPhee, 1996). Only three specimens of Curtonotidae were found among several hundred thousand pieces of fossiliferous Dominican amber, so these flies are quite rare in the amber. Minimal preparation was required of specimen DR14–512, a rather large piece of amber containing a large *Curtonotum* specimen in the center. Specimens DR11–7 and DR11–10 were trimmed into small blocks to produce flat surfaces that optimized frontal, dorsal, and lateral views of these much smaller flies. Trimming was undertaken using methods described in Nascimbene and Silverstein (2000). No specimen was embedded in epoxy for this study, although all will eventually be embedded in EpoTek epoxy for purposes of conservation. The resolution of minute structures can be markedly improved for microscopic study by simply applying to the upper surface of the amber piece a drop of glycerine and then a small coverslip; this reduces distortions from fine surface imperfections. Measurements were made with ocular reticules on a Leitz® Wetzlar stereomicroscope (for tiny structures) and a Zeiss® SV8 stereomicroscope (larger structures). Illustrations were made using camera lucida attachments for each of these microscopes. Photomicrographs were made using Infinity® lenses with a Nikon® D1X camera and MicrOptics® fiber optic flash units. The amber pieces were positioned for measurements, drawings, and photomicrography in a small piece of dental wax applied to a glass microscope slide. Morphological terminology follows that of McAlpine (1981) and Cumming and Wood (2009). Specimens are deposited in the amber collection of the Division of Invertebrate Zoology, American Museum of Natural History.

All measurements are in millimeters (mm).

SYSTEMATICS

Genus *Curtonotum* Macquart

TYPE SPECIES: *Musca gibba* Fabricius, 1805 (preoccupied by *Musca gibba* Rossi, 1794; *Curtonotum taeniatum* Hendel, 1913, proposed as replacement name by Thompson and Pont, 1993).

Curtonotum †electrodominicum, new species

Figures 1–4

DIAGNOSIS: Frons unicolorous golden, fronto-orbital plates surrounding just bases of fronto-orbital setae; anterior reclinate seta minute, lying medial to proclinate and anterior to

posterior reclinate. Thorax barely hunchbacked, light and unicolorous, without dark spots at bases of setae and setulae; notopleural area bare of acrostichals; scutellum without smaller (median) pair of marginal setae; profemur with well-developed ctenidium. Wing infuscate, C with intermittent, large spinules; crossvein dm-cu strongly oblique and slightly sinuous; anal lobe developed (not parallel to vein A); lower calypter not expanded. Female cerci without stout peglike setae (male unknown).

DESCRIPTION: Overall length ca. 7. *Head:* Eye large, depth 1.40, width 0.95, egg shaped in full lateral view, bare, no differentiation of facets. Frons as preserved apparently unicolorous golden microtomentose, with scattered fine setulae; fronto-orbital plates smooth, restricted to bases of fronto-orbital setae. Bases of ipsilateral proclinate and reclinates very close together; proclinate and posterior reclinate large and thick; anterior reclinate minute, lying just medial to proclinate, anterior to posterior reclinate. Base of posterior reclinate orbital seta lying posteromedial to base of proclinate; bases of orbital setae positioned on posterior $\frac{1}{3}$ of frons, near vertex. Ocellar setae well developed, 0.80 length, tips extended to level of lunule; bases lying in middle of ocellar triangle; postocellars slender, erect, cruciate for ca. $0.20 \times$ their length. Medial vertical setae very long, convergent; lateral vertical setae divergent; bases of ipsilateral verticals separated by distance approximately equal to diameter of medial vertical socket. Relative lengths of large orbital setae: medial vertical > ocellar > reclinate = lateral vertical > proclinate > postocellar. Antennal pedicel with several short, stout, black setae dorsally, with lateral seam. Basal flagellomere (antennal article 3) short, length ca. $0.4 \times$ that of arista. Antennal arista with small, cylindrical basal article, main terminal article with long, numerous branches, 9 dorsal,

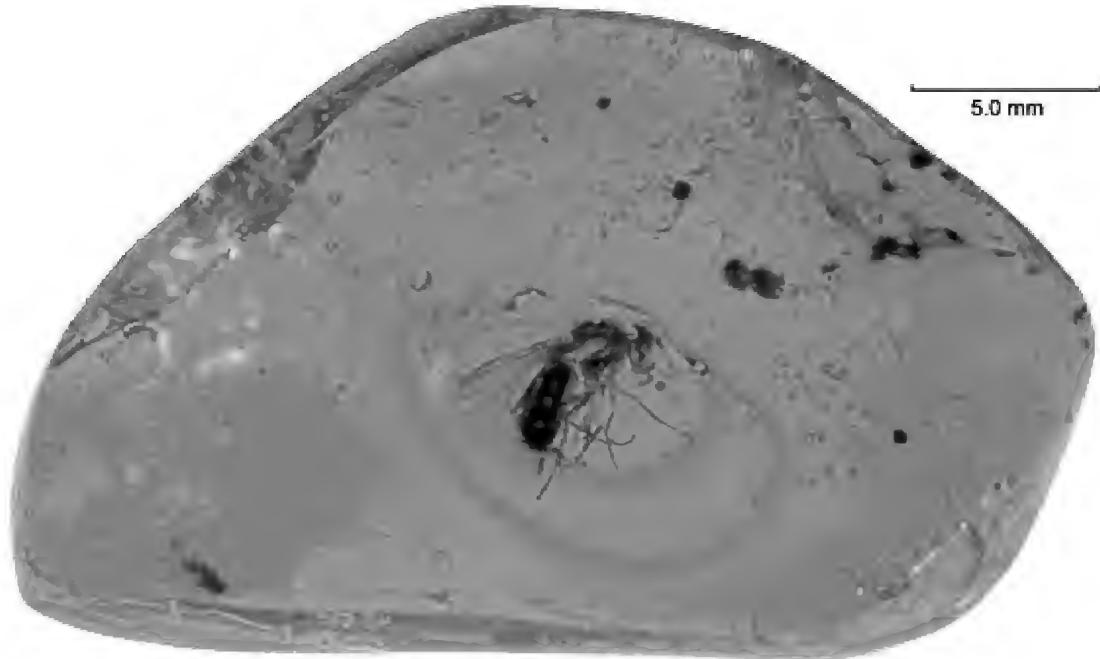


FIG. 1. Holotype of *Curtonotum electrodominicum*, sp. n. (AMNH DR14-512), in amber piece prior to preparation.

5 ventral (excluding small terminal fork). Face slightly bulging medially (not flat), with row of parafacial setae on lower/ventral half of face, flanking carina; parafacials upturned, topmost parafacial (vibrissa) slightly thicker and ca. 2× length of other (ventral) parafacial setae; pair of slightly stouter setae on angle where cheek and gena meet. Clypeus shallow, very dark. Cheek very shallow, light. Palp cylindrical, ventral margin with row ca. 8 fine, stiff setulae; does not appear significantly darker than most of face. Proboscis well developed, labium setose, with 3 pairs fine, stiff setae. Labellum large, length and width appear to occupy most of oral cavity; each lobe with approximately 14 pseudotracheae.

Thorax: Length 3.1; mesoscutum not significantly humpbacked; setae and setulae apparently without dark spots at base; thorax uniformly light colored. Macrosetae: 2 large postpronotals (equal in size); 3 large notopleural setae (equal in size, 2 just above notopleural suture, 1 dorsad); 3 large supraalars (posteroventral one shortest, posterodorsal one largest); 2 pairs dorsocentrals, anterior pair shorter (length 0.85 vs. 1.12 for posterior dorsocentrals), distance between bases of ipsilateral dorsocentrals approx. 0.5× length of anterior dorsocentral; 1 pair prescutellars, length slightly greater than that of anterior dorsocentral; 2 pairs thick scutellar setae, anterior

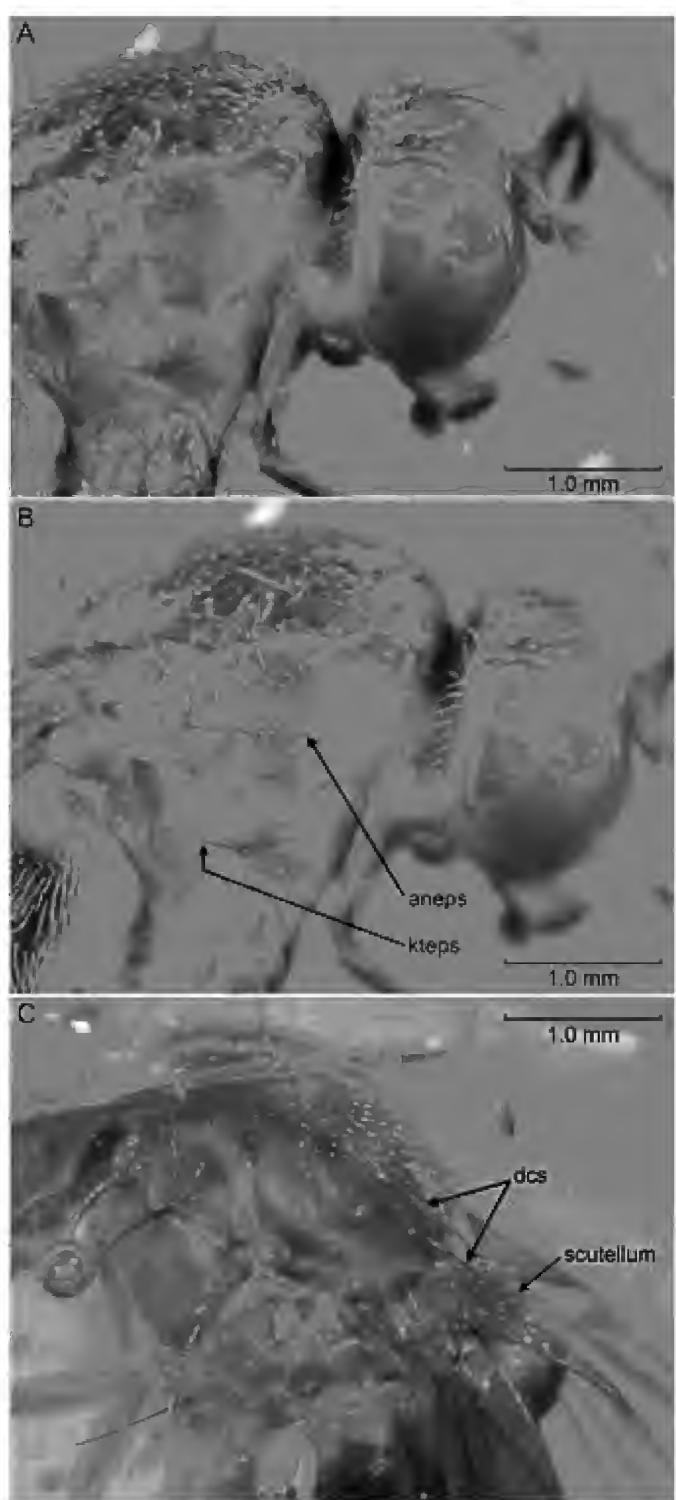


FIG. 2. *Curtonotum electrodominicum*, sp. n., holotype, photomicrographs. A–B. oblique right lateral views of head and thorax, in two focal planes. C. Left dorsolateral view of thorax.

pair divergent (length 1.37), posterior/apical pair cruciate at tips, length 1.07; without small, median pair of scutellar setae; anepisternum with 2 large reclinate setae (lengths 0.65) on posterior margin and 2 small setae (ca. 0.3× the size) on posterodorsal corner; 1 large katepisternal seta (length 0.90). Setulae: acrostichals extensively covering scutum and portion of scutellum, reaching laterally to edge of notopleural and into supraalar areas (notopleural area—demarcated by triangle formed from 3 macrosetae—is bare), acrostichals in 8 uneven rows between dorsocentrals; setulae covering posterior ¾ of scutellum, dorsally and laterally, marginal setulae longer; anepisternum with 22–24 fine setulae; katepisternum with ca. 5–6 fine setulae, row of thicker setulae on posteroventral margin. Posterior thoracic spiracle without fringe of setulae on posteroventral margin.

Wing: Length 4.7. Lightly infuscate gray-brown, heaviest surrounding apices of R_{2+3} and R_{4+5} , and in cell d. C spinose, with lateral row of slightly larger, thicker, erect spinules on proximal half of C; costal spinules end midway between apices of R_{2+3} and R_{4+5} , C ends at apex of M; Sc complete, fine, adjacent to R_1 ; apex of R_{4+5} ends at tip of wing; crossvein br–m very short, length ca. 2× thickness of M; apical halves of R_{2+3} , R_{4+5} and M virtually parallel (not divergent); crossvein dm–cu strongly oblique and slightly sinuous; length of distal section of Cu slightly longer than crossvein dm–cu; anal lobe small, but present (anal margin not parallel to vein A); vein A thick, well developed, almost meeting margin of wing; lower calypter not expanded; anal lobe not highly reduced. Halter light.

Legs: Apparently without color patterns. Procoxa long, nearly equal in length to profemur, mesodistal margin with 2 thick, black setae; profemur with lateral row short, fine setae, 1 long, erect seta medially; mesal surface of profemur with longitudinal ctenidium of 16 small, black, spiniform setulae; protibia with setulae in longitudinal rows dorsally, mesally with 5–6 transverse, shingled rows of setulae apically, forming combs, with short, stout preapical seta; protarsus with thicker setulae ventrally, probasitarsomere slightly longer than protibia, with 3 thick, procurved setae at base. Protarsi with claws simple (not toothed), pulvilli well developed. Mesocoxa with transverse row long, thick, black setae on anterior surface; mesofemur with setulae on dorsal surface not in rows, anterior surface with row of 4 thick setae on distal half, ventrally with longitudinal row of ca. 12 thicker, decumbent setae, distal end of femur with pair of preapical setae on lateral surfaces; mesotibia with setulae in longitudinal rows, with 4 pre-/apical thick setae; mesotarsus with setae in longitudinal rows, ventrally with 2 longitudinal rows thick, short setae, apices of each tarsomere with 4 slightly larger setae. Metacoxa with single large lateral seta, several smaller ones, dorsal setulae not in rows, with stiff, dorsopreapical seta; metatibia with small apical seta, transverse comb of minute setae on ventroapical margin; metadistitarsomere without stout “cuneiform” setulae on ventral surface.

Abdomen: Tergite I short, entirely light, without dark markings; tergites II–V large, with extensive dark markings over most of each tergite, with pair of light, microtomentose areas anterolaterally (these areas devoid of setae or setulae); tergite II with row of ca. 10 erect setulae on posterior border of microtomentose area; sternites well developed, distal halves of sternites IV and V and most of VI dark; segments VI–VIII small, telescoping. Female cerci slender, possibly dorsoventrally flattened and connected anterodorsally (to tergite X?), but

not heavily sclerotized posteriorly, cerci without stout, peglike setae; sternite VIII apparently not differentiated from other sternites (i.e., not dorsoventrally flattened), though cryptic. Internal reproductive organs not observed.

TYPE: Holotype ♀, Dominican Republic, AMNH DR14-512, from amber mines in Cordillera Septentrional, northern Dominican Republic (Miocene). Specimen is complete and very well preserved, although dorsomedial portions of the fly are obscured due to a conchoidal fracture surrounding the fly. The fly lies in the middle of a transparent 37 × 23 × 10 mm piece of amber, which also contains numerous bubbles, some particulate debris, and a female ceratopogonid.

ETYMOLOGY: From the Greek *electron*, for “amber,” and *dominicum*, in reference to the country of origin.

COMMENTS: Inference on the phylogenetic relationships of *C. electrodominicum*, sp. n., can be made based on the work by Klymko and Marshall (2011) and Kirk-Spriggs and Wiegmann, in prep. The clade of approximately eight species of North American and Eurasian *Curtonotum* (the *Anus* species group) can be excluded, as the fossil has female cerci unfused to tergite X, the cerci do not bear peglike setae, and the orbital setae are confined to the distal posterodorsal third of the frons. Spermathecae (i.e., shape, capsule texture, duct length) are not visible in the fossil, but the fossil shares features with the large Neotropical clade, *Curtonotum* sensu stricto (Klymko and Marshall, 2011), which these authors divided into several species complexes. The *Murinum* species complex can be excluded as the fossil does not possess three pairs of marginal scutellar setae, nor is the lower calypter lobed. The *Taeniatum* species complex can be excluded as the fossil does not bear setae on the posterior margin of the mesothoracic spiracle. *Curtonotum electrodominicum*, sp. n., conforms most to the *Vulpinum* species complex since microtomentum on the frons is restricted to the bases of the orbital setae and metatarsomere 5 does not possess cuneiform setulae. The *Vulpinum* species complex contains nine species (seven undescribed) distributed from southern Mexico to northern Bolivia (Klymko and Marshall, 2011). The fossil, however, possesses a small anal lobe of the wing as in the Nearctic species *C. helvum* (Loew) and *C. floridense* Klymko and Marshall and many Afrotropical species and unlike that in Neotropical *Curtonotum* (wherein the anal margin of the wing lies close and parallel to the anal vein). There are also three distinctive features of *C. electrodominicum*, sp. n., all of them wing features: the outer/lateral edge of vein C possesses a row of ca. 30 erect spinules, instead of the typical 5–6 interspersed among the decumbent spinules; crossvein dm–cu is substantially oblique to veins M and CuA (rather than approximately perpendicular to them) and this crossvein is convex rather than straight. The last two features, regarding crossvein dm–cu, commonly occur in species of the Afrotropical region (e.g., *Curtonotum keiseri* Tsacas, *C. stuckenbergi* Tsacas, and *C. parkeri* Kirk-Spriggs, which are placed into a *Stuckenbergi* species group by Kirk-Spriggs and Wiegmann, in prep.). The placement of the orbital setae near the posterodorsal portion of the head is a feature that the fossil shares with a different Afrotropical lineage (the *Striatifrons* species group, sensu Tsacas, 1977): *C. herrero* Tsacas, *C. striatifrons* Malloch, and what is currently referred to as *C. tigrinum* Séguy.

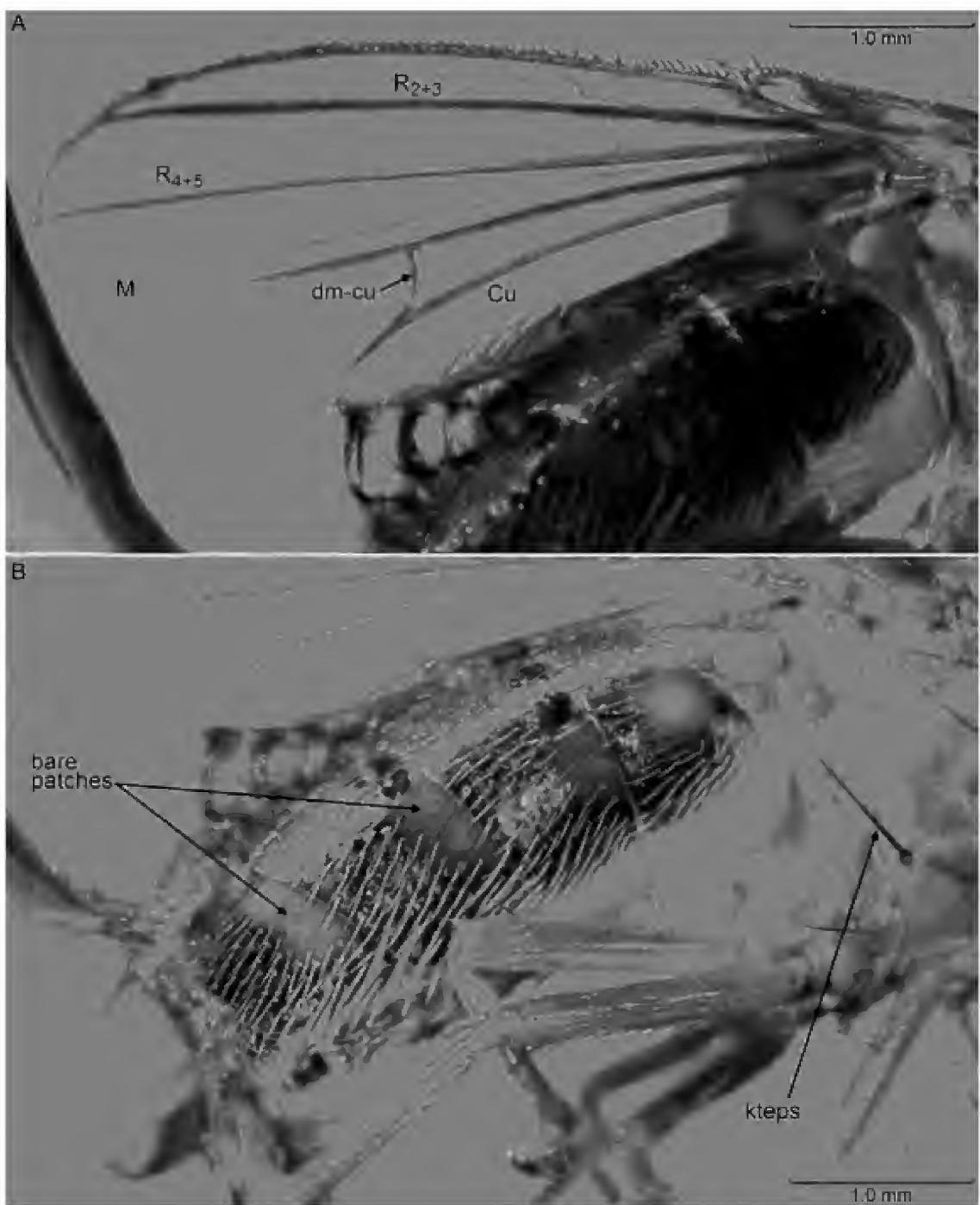


FIG. 3. *Curtonotum electrodominicum*, sp. n., holotype, photomicrographs. A. Wing. B. Abdomen and posterior portion of thorax. Thickness of whitish setae on ventrolateral portion of tergites IV–V appears to be preservational. Abbreviation: **ktep**, katepisternal setae.

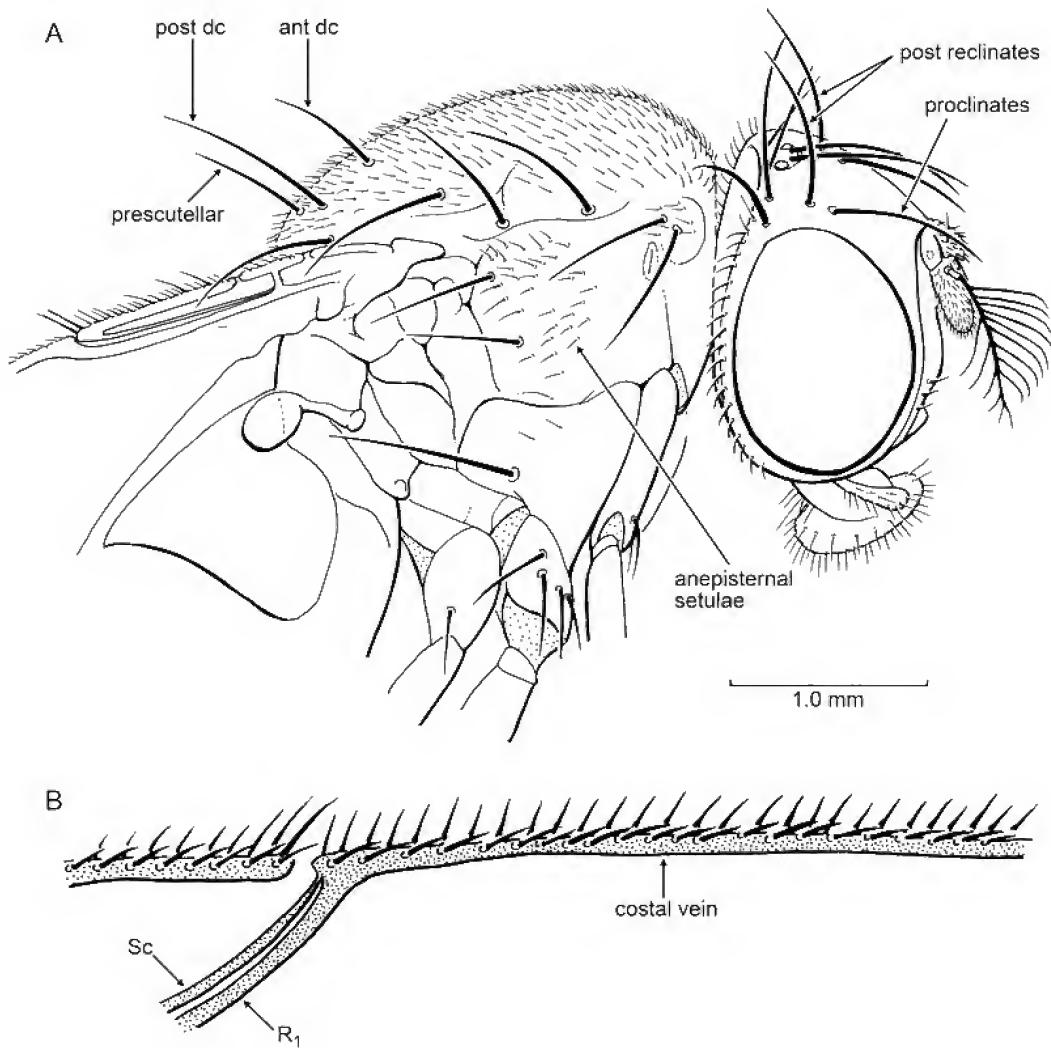


FIG. 4. *Curtonotum electrodominicum*, sp. n., holotype, drawings. A. Head and thorax in right lateral view, with positions and orientations of orbital setae reconstructed as they would have been in life. B. Detail of costal chaetotaxy. Abbreviations: **ant**, anterior; **dc**, dorsocentral; **post**, posterior.

Depressonotum, new genus

DIAGNOSIS: Small, overall length 2.77; arista with long dorsal and ventral branches; orbital setae confined to posterodorsal $\frac{1}{3}$ of frons, anterior recline seta minute; thorax light and unicolorous (bases of setae surrounding sockets possibly with very faint dark spots), scutum hardly "humpbacked." Postpronotal lobe with 1 strong seta; anepisternum with 2 large recline setae; scutellum with 2 pairs of large marginal setae (median setulae only slightly larger than those on disc); scutellar disc with setulae. Wing: base of vein C beyond Sc break with row of ca. 14 larger, semierect spinules on ventral edge; wing largely hyaline, with slight infuscation on costal edge in male; crossvein dm-cu perpendicular to M (not oblique), distant from wing margin; vein A well

developed, apically evanescent; anal margin of wing parallel to vein A. Male abdomen slender, tergite VII dorsally with pair of large, erect setae; surstyli curved, apically narrowed, bare; female cercus slender, oval, without peglike setae and apparently not fused to tergite X.

TYPE SPECIES: *Depressionotum priscum*, sp. n., known only in Miocene amber from the Dominican Republic. By original designation.

ETYMOLOGY: From the Latin *depressum* ("flattened") and *-notum* (a common suffix of genera in the family), in reference to the primitively flat thorax of this fly.

Depressionotum priscum, new species

Figures 5, 6

DIAGNOSIS: As for genus.

DESCRIPTION: *Head*: Eye large, occupying most of head in profile, bare, without differentiation of facets, egg shaped (narrower portion ventrally); depth 0.51 (male), 0.56 (female), width 0.40 (male) 0.36 (female). Antenna light colored; pedicel with well-developed dorsolateral seam, anterior surface with 4–5 thicker setulae, row of 5 stout, black spinules on ventromesal margin; basal flagellomere relatively short, length ca. 2× that of pedicel; arista with short, ringlike basal article, base of main (branched) portion slightly swollen, arista with 5–6 long dorsal branches (curved apically), 2–3 ventral branches (exclusive of terminal fork). Proclinate and posterior reclinate fronto-orbital setae well developed, bases separated by distance only slightly larger than diameter of sockets; anterior reclinate extremely minute, lying between large fronto-orbitals, all fronto-orbitals lying on posterior ½ of frons. Ocellar setae long, divergent, bases lying within ocellar triangle; postocellars slightly cruciate; medial vertical setae extremely long, convergent (tips almost crossing), lateral verticals divergent. Lengths of orbital and vertical setae: medial verticals (0.40 male, 0.43 female) > posterior reclinates = lateral verticals > ocellars > proclinates > postocellars. Frons unicolorous golden; no sexual dimorphism in proportions. Vibrissae well developed, approximately 3× size of subvibrissal setulae; cheek light, very shallow; mouthparts light; palps long and slender (length >5× width), slightly curved, with ventral row of 7 fine, stiff setulae.

Thorax: Length 1.05 (male), 1.225 (female). Mesoscutum not hunchbacked, unicolorous light, setae and setulae possibly with faint darker spots at base surrounding sockets. Acrostichals cover most of scutum, in approximately 6 irregular rows between dorsocentrals, notopleural area bare. Two pairs of dorsocentral setae, anterior pair relatively small (ca. ½ thickness and length of posterior dorsocentrals), lengths in: 0.215 (male), 0.292 (female); posterior dorsocentrals: 0.473 (male), 0.593 (female). Pair of well-developed prescutellar setae present (3.5× length of acrostichals); lateral scutellars significantly larger (1.4× the length) than apical pair (0.43); postpronotal lobe with one large seta; notopleural area with 3 large setae, including presutural one dorsally (this seta smaller in female: 0.30 in male, 0.258 in female); 3 supraalar setae present, 2 lateral ones longer and finer. Anepisternum with 2 long setae on posterior margin, recurved posteriad; also with 8–9 fine, stiff setulae scattered over surface; katepisternum with single large setae, 3–4 setulae.

Wing: Length 2.25 (male), 2.30 (female). Entirely hyaline in female, with slight infuscation on leading (costal) ⅓ of wing membrane in male. Vein C ends at apex of vein M; costal spinules end midway between apices of R_{2+3} and R_{4+5} ; base of C distal to Sc break with row of ca. 14

larger, semierect spinules on ventral edge. Vein R_{4+5} terminates at wing apex, apical halves of M and long R veins virtually parallel (not significantly convergent or divergent). Crossvein br–m very short, length $2.5 \times$ diameter of longitudinal veins; crossvein dm–cu long, perpendicular (not oblique) to vein M, straight (not sinuous or concave); length of apical portion of vein Cu (from intersection with dm–cu) $1.3 \times$ length of dm–cu. Vein A well developed, apically evanescent; anal lobe barely developed, extremely shallow; anal margin parallel and close to vein A. Halter entirely and very light colored.

Legs: No discernable sexual dimorphism. Procoxa with thick, curved seta on fronto-apical margin; profemur with mesal ctenidium of 4–6 spinules (more closely spaced apically), lateral surface with 2 stiff, fine setae; protibia with stout, dorsal, preapical seta; protibia also with 3 short, transverse, apical/preapical combs of setulae on mesal surface; protarsus densely setulose, basitarsomere slightly shorter than combined length of distal tarsomeres. Mesocoxa with row of 3–4 thick, curved setae on ventral margin; mesofemur with pair of short, stout, preapical setae, one each on anterior and posterior surface, row of 3–4 semierect setae on dorsal surface; mesotibia with 1 apical seta (on ventral surface) and 2 preapical setae (on lateral and mesal surfaces); mesotarsomeres each with pair of ventral rows of minute cuneiform setulae. Metacoxae slightly longer in male, with lateral seta in both sexes; metafemur and metatibia with dorso-preapical seta; metatarsus as for mesotarsus.

Abdomen: Female with tergites and sternites unicolorous light brown, setose, but without microtrichia or microtomentum (and so probably shiny); tergites II–V largest, tergite VI less than half the size of V, with slight anteromedial desclerotization; segments VII–X small, telescoping; cerci slender, ovoid, length $2.7 \times$ width, without peglike setae (only fine setulae); cerci separate from each other and tergite X. Internal reproductive organs of female not observable. Male with abdomen slender, tergites II–VI extended ventrolaterally, dorsal portions of tergites with darker infuscation; ventrolateral margins of tergites III–V with row 4–5 thicker, stiff, spinulelike setae; tergite V with dorsoapical margin slightly V-shaped; tergite VII with pair of large, erect, divergent setae (length 0.241); epandrium apparently relatively short; surstyli bare, narrowed apically, curved posteriad, bearing minute, but stout subapical setula; cercus hemispherical, with marginal fringe of long setae; postgonites lying immediately medial to surstyli; aedeagus (basal portion visible through cuticle from fly's right side) long and arched.

TYPES: Holotype ♂, AMNH DR11–7, in Miocene amber from the Cordillera Septentrional of the Dominican Republic, purchased from Manuel Perez. The specimen is complete and well preserved in a clear yellow piece of amber that has been trimmed and polished into a small rectangle $5 \times 4 \times 3$ mm in size, maximizing dorsal, frontal, posterior, and lateral views. Fortunately, the cuticle on the apical segments is somewhat cleared on the fly's right side, allowing an internal view of the distal portion of the aedeagus. Microtomography may eventually provide a detailed view of the internal genitalia. Paratype ♀, AMNH DR11–10, same data as holotype. This specimen is likewise complete and well preserved, in a piece of amber $6 \times 5 \times 3$ mm, although a halo of discoloration in the amber that surrounds the fly obscures some details of the median portion of the body.

ETYMOLOGY: From the Latin *priscus*, “ancient.”

COMMENTS: The pair of setae on male tergite VII is a feature distinctive to some recent Diastatidae (*Euthychaeta spectabilis* (Loew), some *Campichoeta* Macquart and *Diastata* Meigen), as

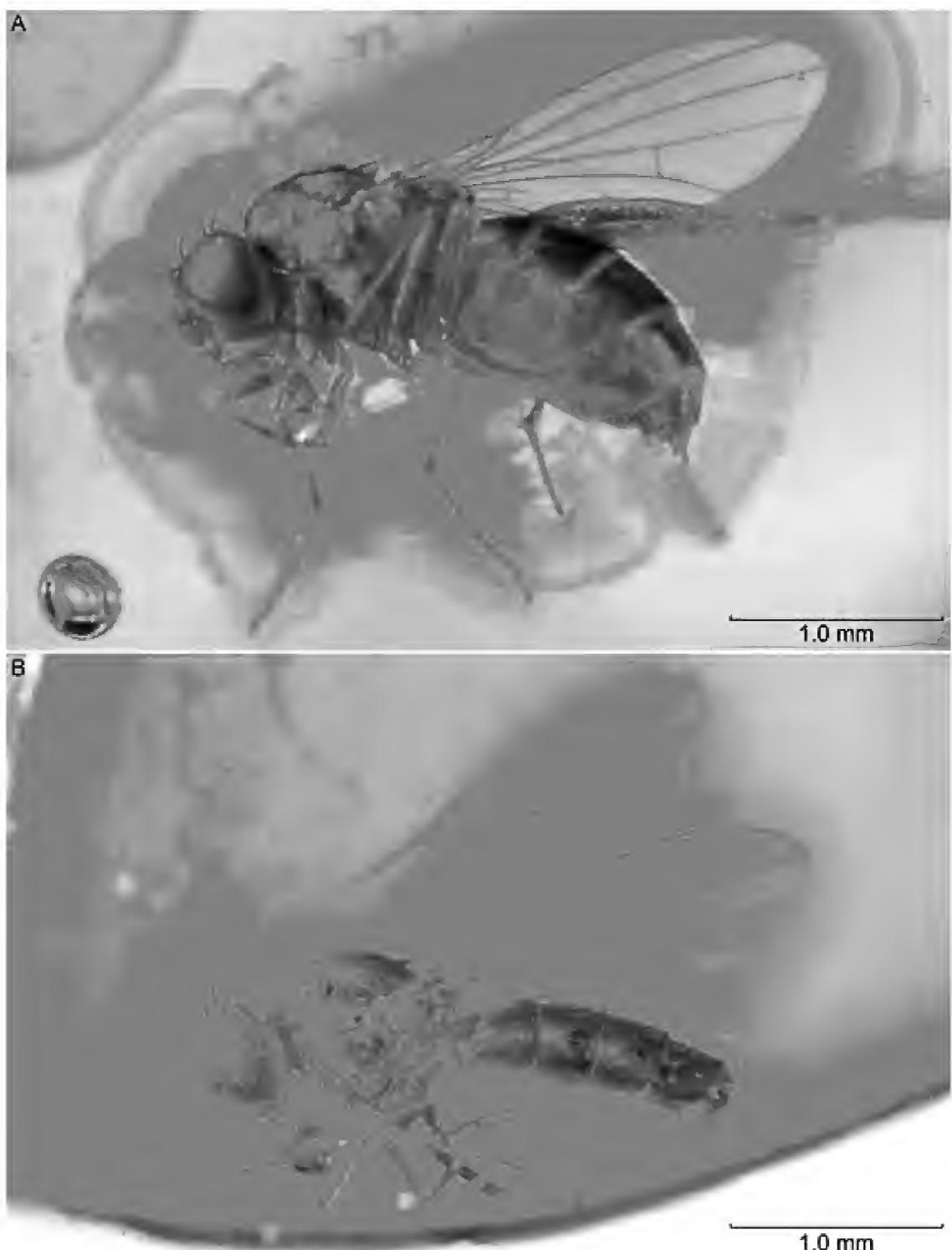


FIG. 5. *Depressonotum priscum*, gen. et sp. n., photomicrographs. A. Female paratype, AMNH DR11-10. B. Male holotype, AMNH DR11-7.

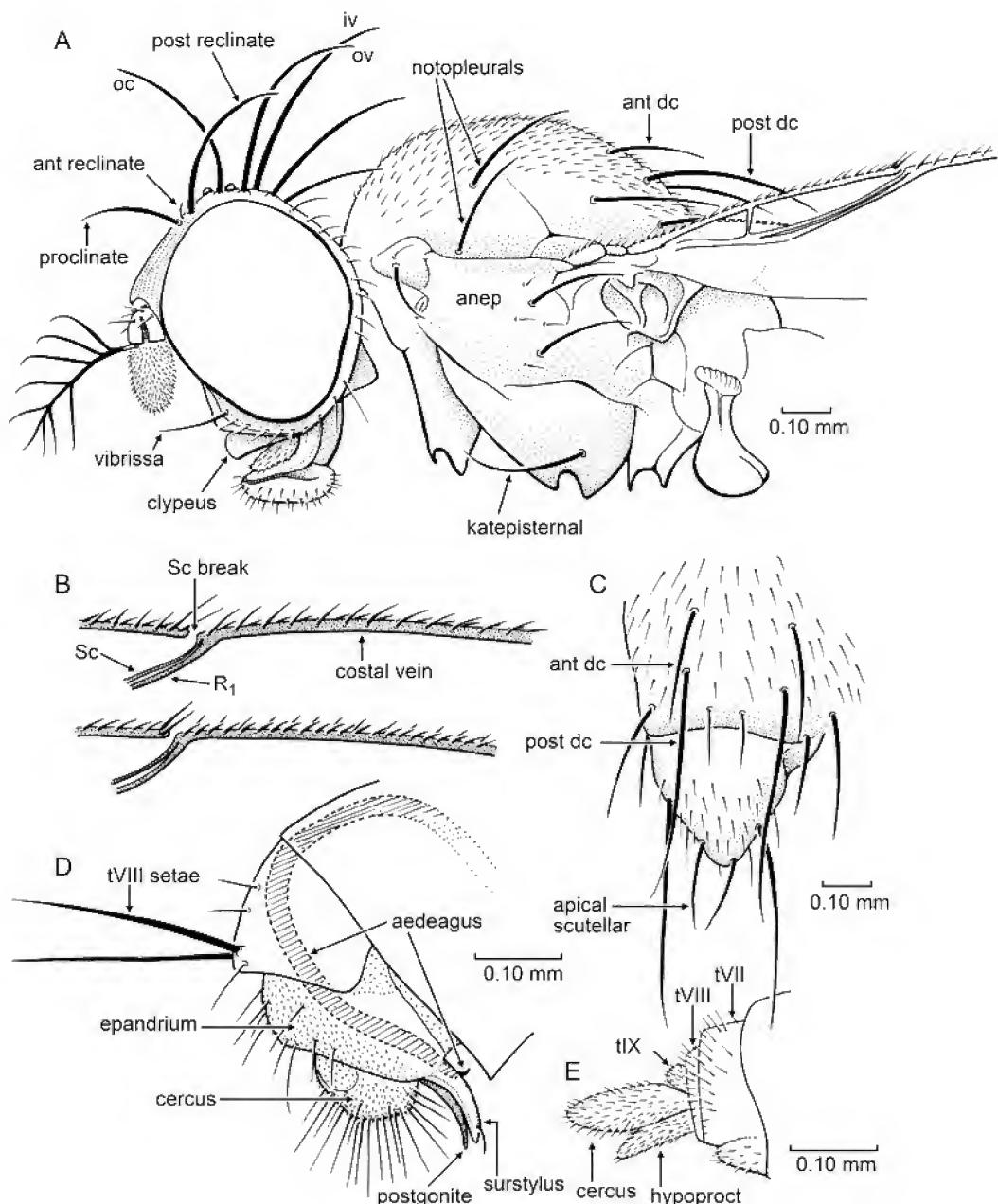


FIG. 6. *Depressonotum priscum*, gen. et sp. n., details, as illustrated with male holotype (A-D) and female paratype (E). A. Head and thorax, left lateral view. B. Basal sections of vein C, showing chaetotaxy of lateral/lower edge (above) and mesal/upper edge (below). C. Posterior portion of thorax in dorsal view, including scutellum and showing setation. D. Right lateral view of male terminalia, showing underlying aedeagus. E. Female terminalia, right lateral view. Abbreviations: **anep**, anepisternum; **ant**, anterior; **dc**, dorsocentral seta; **iv**, inner (medial) vertical seta; **oc**, ocellar seta; **ov**, outer (lateral) vertical seta; **post**, posterior; **tVII**, **tVIII**, **tIX**, tergites VII, VIII, IX.

well as the species of *Pareuthyshaeta* Hennig in Baltic amber, but this feature also occurs in *Curtonotum herrero*, *C. striatifrons*, and *C. tigrinum*. There is little doubt that *Depressonotum*, gen. n., is a curtonotid. The fossil species apomorphically possesses long branches on the arista (short to long pubescent in diastatids), a setulose anepisternum and scutellum (lacking in diastatids), a well-developed profemoral ctenidium; a short row of larger, semierect spinules on vein C (otherwise occurs only in *Diastata*); a long, arched aedeagus (distinctive to Curtonotidae); and a complete Sc. A complete Sc was considered an autapomorphy of Curtonotidae by Kirk-Spriggs and Wiegmann, in prep., but it may be plesiomorphic since it also occurs in the Eocene genus *Pareuthyshaeta* (Grimaldi and Singh, 2012) and more basal Schizophora (i.e., Tephritoidea). Definitive plesiomorphic features of *Depressonotum* are the scutal shape, presence of a pair of prescutellar setae, only two pairs of marginal scutellar setae, and a crossvein dm–cu that is distant from the wing margin (by a distance greater than the length of the vein). This crossvein is close to the wing margin in most curtonotids (all except *Axinota* and *Cyrtona*).

It is important to consider the occurrence of these apomorphic features among Ephydriidea in general. Long branches on the arista occur in most Drosophilidae, some derived Camillidae, some Ephydriidae, and most Curtonotidae (short branches occur in most species of *Cyrtona* sensu lato). Grimaldi (1990) postulated that long dorsal and ventral aristal branches constituted a synapomorphy of Curtonotidae and Drosophilidae, since the crowded, long branches in *Leucophenga* Mik and other genera of the more plesiomorphic subfamily, Steganinae, are very similar to those of Curtonotidae. Otherwise, morphological differences of a plumose arista suggest convergence among families of ephydroids. Such an arista in some Ephydriidae, for example, always has just dorsal branches. In a lineage of Camillidae comprised of the genera *Afrocamilla* Barraclough, *Camilla* Haliday, and *Teratocamilla* Barraclough, the long branches of the plumose arista are much fewer in number. Diastatidae always have an arista with short to long pubescence or with very short branches.

Setulae on the scutellar disk are very distinctive and occur in *Curtonotum* and *Axinota* of the Curtonotidae; *Katacamilla* Papp (but not in other Camillidae, even the Eocene genus *Protocamilla* Hennig); and assorted, unrelated Ephydriidae. Scutellar setulae do not occur in Diastatidae or Drosophilidae, and so may be an apomorphic feature for Curtonotidae.

In summary, *Depressonotum* uniquely combines features that are plesiomorphic within the Ephydriidea and ones that are apomorphic (i.e., possessed by some or all Curtonotidae). In lieu of a formal phylogenetic analysis, it probably occupies a very basal position within Curtonotidae, and certainly shows no obvious relationships with known genera.

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REFERENCES

Chandler, P.J. 1987. The families Diastatidae and Campichoetidae (Diptera, Drosophiloidea), with a revision of Palaearctic and Nepalese species of *Diastata* Meigen. *Insect Systematics and Evolution* 18: 1–50.

Cumming, J., and D.M. Wood. 2009. Adult morphology and terminology. *In* B.V. Brown et al. (editors), *Manual of Central American Diptera*, vol. 1: 9–50. Ottawa: National Research Council Press.

Delfinado, M. 1969. The Oriental species of Curtonotidae (Diptera). *Oriental Insects* 3: 199–219.

Greathead, D.J. 1958. Notes on the larva and life history of *Cyrtotomum cuthbertsoni* Duda (Dipt., Drosophilidae), a fly associated with the desert locust *Schistocerca gregaria* (Forskål). *Entomologist's Monthly Magazine* 94: 36–37.

Grimaldi, D. 1987. Amber fossil Drosophilidae (Diptera), with particular reference to the Hispaniolan taxa. *American Museum Novitates* 2880: 1–23.

Grimaldi, D. 1989. Amber fossil Drosophilidae (Diptera), part II. Review of the genus *Hyalistata*, new status (Steganinae). *American Museum Novitates* 3084: 1–15.

Grimaldi, D. 1990. A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). *Bulletin of the American Museum of Natural History* 197: 1–139.

Grimaldi, D.A. 1995. The age of Dominican amber. *In* K.B. Anderson and J.C. Crelling (editors), *Amber, resinite, and fossil resins: 203–217*. American Chemical Society Symposium Series 617. Washington, D.C.

Grimaldi, D.A. 2005. A stalk-eyed ephydroid fly from the Eocene (Diptera: Ephydrioidea: Camillidae). *Proceedings of the Entomological Society of Washington* 110: 543–550.

Grimaldi, D.A., and J. Cumming. 1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum of Natural History* 239: 1–124.

Grimaldi, D.A., and M.S. Engel. 2005. *Evolution of the insects*. New York: Cambridge University Press.

Grimaldi, D., and H. Singh. 2012. The extinct genus *Pareuthyochaeta* in Eocene ambers (Diptera: Schizophora: Ephydrioidea). *Canadian Entomologist* 144: 17–28.

Grimaldi, D., and B. Underwood. 1986. *Megabraula*, a new genus for two new species of Braulidae (Diptera), and a discussion of braulid evolution. *Systematic Entomology* 11: 427–438.

Hennig, W. 1958. Die Familien der Diptera Schizophora und ihre phylogenetischen Verwandtschaftsbeziehungen. *Beiträge zur Entomologie* 8: 505–688.

Hennig, W. 1965. Die Acalyptratae des baltischen Bernsteins und ihre Bedeutung für die Erforschung der phylogenetischen Entwicklung dieser Dipteren-Gruppe. *Stuttgarter Beiträge zur Naturkunde, Serie C, Allgemeinverständliche Aufsätze* 127: 1–215.

Iturrealde-Vinent, M.A., and R.D.E. MacPhee. 1996. Age and paleogeographical origin of Dominican amber. *Science* 273: 1850–1852.

Kirk-Spriggs, A.H. 2007. A reappraisal of the type fossil of *Curtonotum †gigas* Théobald 1937 (Diptera: Curtonotidae), a compression fossil of Early Oligocene age from Provence, France. *Annals of the Eastern Cape Museums* 6: 13–20.

Kirk-Spriggs, A.H. 2008a. Order Diptera, family Curtonotidae. *In*: van Harten, T. (Ed.), *Arthropod fauna of the United Arab Emirates*. Volume 1. Dar al Ummah Publishing, Abu Dhabi, pp. 704–713.

Kirk-Spriggs, A.H. 2008b. A contribution to the knowledge of the immature stages of *Curtonotum* (Diptera: Curtonotidae), from Africa and the Middle East, with a discussion of relationships to other known Ephydrioidea larvae. *African Entomology* 16: 226–243.

Kirk-Spriggs, A.H. 2010a. A revision of the Afrotropical Quasimodo flies (Diptera: Curtonotidae: Schizophora). Part I – the genus *Axinota* van der Wulp, with the description of three new species. *African Entomology* 18: 99–126.

Kirk-Spriggs, A.H. 2010b. A revision of the Afrotropical Quasimodo flies (Diptera: Curtonotidae: Schizophora). Part II – the East African Afromontane genus *Tigrisomyia* gen. n., with descriptions of four new species. *African Entomology* 18: 127–146.

Kirk-Spriggs, A.H. 2011. A revision of the Afrotropical Quasimodo flies (Diptera: Schizophora: Curtonotidae), Part III. The Malagasy species of *Curtonotum* Macquart, with descriptions of six new species. *African Invertebrates* 52: 391–456.

Kirk-Spriggs, A.H., and A. Friedberg. 2007. The Palaearctic species of Curtonotidae (Diptera: Schizophora), with special reference to the fauna of Israel. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique (Entomologie)*. 77: 133–146.

Kirk-Spriggs, A.H., and B. Wiegmann. In prep. A revision of Afrotropical Quasimodo flies (Diptera: Schizophora; Curtonotidae). Part IV – the continental Afrotropical species of *Curtonotum* Macquart, with description of 13 new species, a combined phylogenetic analysis, and revised classification of the Curtonotidae.

Kirk-Spriggs, A.H., M. Kotrba, and R.S. Copeland 2011. Further details of the morphology of the enigmatic African fly *Mormotomyia hirsuta* Austen (Diptera: Mormotomiidae). *African Invertebrates* 52: 145–165.

Klymko, J., and S.A. Marshall. 2011. Systematics of New World *Curtonotum* Macquart (Diptera: Curtonotidae). *Zootaxa* 3079: 1–110.

McAlpine, D.K. 2011. Observations on the antennal morphology in Diptera, with particular reference to the articular surfaces between segments 2 and 3 in the Cyclorrhapha. *Records of the Australian Museum* 63: 113–166.

McAlpine, J.F. 1981. Morphology and terminology – adults. In J.F. McAlpine et al. (editors), *Manual of Nearctic Diptera*, vol. 1: 9–64. Research Branch Agriculture Canada Monograph 27, Ottawa.

McAlpine, J.F. 1989. Phylogeny and classification of the Muscomorpha. In J.F. McAlpine (editor), *Manual of Nearctic Diptera* volume 3: 1397–1518. Agriculture Canada Research Branch Monograph 32, Ottawa.

Meier, R., M. Kotrba, and K. Barber. 1997. A comparative study of the egg, first-instar larva, puparium, female reproductive system and natural history of *Curtonotum helvum* (Curtonotidae; Ephydroidea; Diptera). *American Museum Novitates* 3219: 1–20.

Nascimbene, P., and H. Silverstein. 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. In D. Grimaldi (editor), *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey*: 93–102. Leiden: Backhuys.

Théobald, N. 1937. Les insectes fossiles des terrains oligocènes de France. Nancy: G. Thomas.

Tsacas, L. 1974. Étude préliminaire des Curtonotidae de Madagascar (Diptera). *Annales de la Société Entomologique de France* 10: 703–719.

Tsacas, L. 1977. Les Curtonotidae (Diptera) de l'Afrique: 1. Le genre *Curtonotum* Macquart. *Annals of the Natal Museum* 23: 145–171.

Wiegmann, B.M., et al. 2011. Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences of the United States of America* 108: 5690–5695.